Histological characteristics of lower jaw bones and oral teeth of the short nose gar, *Lepisosteus platostomus* Rafinesque, 1820 (Lepisosteidae)

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Abstract. – Lepisosteidae are ram feeding fishes with caniniform teeth on their upper and lower jaws. The teeth are constituted of a cone of dentine with an apical cap of acrodin, and are fixed to the jaw bones by bone of attachment. The external surface of the teeth is ridged from their base till the base of the apical cap. The wall of the pulp cavity, shows radially-oriented folds that are characteristic of plicidentine. The enamel layer takes part in this folding that characterizes the polyplocodonte type of plicidentine. The primary and secondary bone tissue that constitutes the tooth supporting bone are both cellular and they contain canaliculi of Williamson that are frequently branched.

Résumé. – Les caractéristiques histologiques des mâchoires et des dents orales du lépisosté à museau plat, *Lepisosteus platostomus* Rafinesque, 1820 (Lepisosteidae).

Les Lepisosteidae sont des prédateurs ichtyophages qui possèdent des dents caniniformes sur leurs mâchoires supérieures et inférieures. Ces dents sont constituées d'un cône de dentine avec une coiffe d'émail (acrodine) et elles sont ancrées sur la mâchoire par de l'os d'attache. À la base de la dent, la surface externe de la dentine est finement striée et les parois pulpaires montrent des replis de dentine, deux caractéristiques révélant la présence de plicidentine. Cette plicidentine est localisée assez haut dans la cavité dentaire tout en conservant des replis simples, soutenus par des invaginations de l'émail. Ces invaginations dans les plis caractérisent le type polyplocodonte de plicidentine. Le tissu osseux primaire et secondaire des os dentigères renferme des ostéocytes et est traversé par de nombreux canaliculi de Williamson qui peuvent se ramifier plusieurs fois. Le tissu osseux localisé au voisinage des dents est soumis à remaniement.

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The Neopterygii, represented by the Teleostei and the Holostei, form the principal and most derived group among Actinopterygians. Although teleosts are the dominant group since the Late Cretaceous/Tertiary, and now represented by 31,000 living species (Froese and Pauly, 2016), its sister-group, the holosteans, that had their main radiation during the Mesozoic (Hurley *et al*., 2007; Friedman, 2015), still have few living species.

The Super Division Holostei, Müller (1844), is formed by the Ginglymodi (with one extant family, Lepisosteidae) plus the Halecomorphi (with a unique living species, *Amia calva*). Extant lepisosteids, or gars, are restricted to North and Central America, Cuba, and Juventud Island. This family is represented today by seven species within two genera, *Lepisosteus* (5 species) and *Atractosteus* (2 species), which in turn represent the evolutionary remnant of a group that, by the end of the Mesozoic and during the Tertiary, was distributed in South America, Africa, India, Europe, and North America (Brito *et al*., 2006, 2016; Grande, 2010; Nelson *et al*., 2016). This lineage kept its primitive appearance, known since the Mesozoic, and, due to its evolutionary conservatism, has been treated as a classic "living fossil" *sensu* Wiley and Schultze (1984).

Although the two holostean extant families, the Amiidae and the Lepisosteidae, have recently been revised (by Grande and Bemis, 1998 and by Grande, 2010, respectively), these studies were based mainly on skeletal morphology. So the histological study was neglected or treated only superficially; the same being true for the fossil Ginglymodi (Cavin, 2010; López-Arbarello, 2012; Cavin *et al*., 2013). Yet, the nature of the external hypermineralized layer of teeth, *i.e*. the cap of enameloid and the collar enamel, has been recently specified for *Lepisosteus oculatus* (Sasagawa and Ishiyama, 2005; Sasagawa *et al*., 2009, 2014).

Detailed descriptions of the bone tissues supporting teeth, as well as the plicidentine in gar teeth, are scarce and relatively old (Agassiz, 1833-1844; Nickerson, 1893; Möller, 1940; Peyer, 1968; Schultze, 1969) with a few recent contributions (*cf*. Grande, 2010; Germain *et al*., 2016). Yet, Peyer (1968) published an interesting study of the histologi-

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cal structure of labial teeth. His descriptions, reproduced by Grande (2010: fig. 240), were illustrated with fine colour plates but no histological description was given of tooth attachment bone (*cf.* Peyer, 1968). Schultze, describing the plicidentine organization in the teeth of the gar (Schultze, 1969: pl. 20, fig. 1-5), concluded that it belongs to the polyplocodonte type (Schultze, 1970). The spatial organization of plicidentine in gar teeth was also recently confirmed through tomography and virtual modelling (Fig. 1) (Germain *et al.*, 2016).

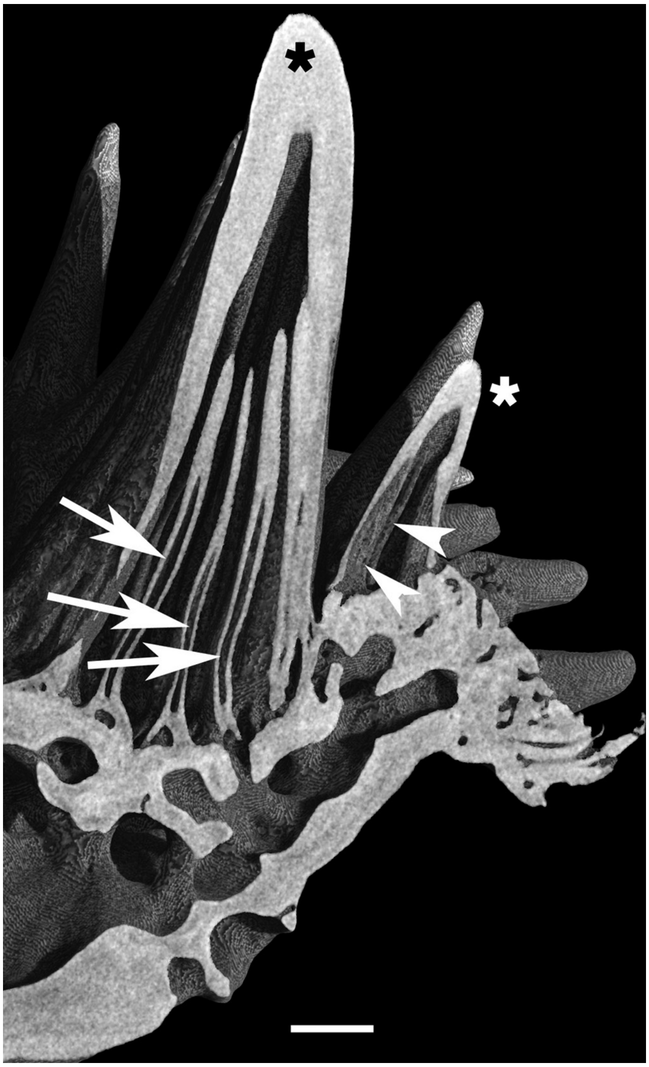

Figure 1. – *Lepisosteus platostomus*. Tomographic image of a fang (black asterisk), and a mid-sized caniniform teeth (white asterisk) in the anterior part of the left lower jaw. The tridimensional reconstruction of the dentary bone and teeth shows three folds in the internal wall of the fang (arrows), which occupy two thirds of the pulp cavity. The space indicated by arrows between the narrow walls of each fold corresponds to external area of the tooth due to the synchronized folding of both the dentine and the collar enamel. The pulp cavity of the second tooth also shows two folds (arrowheads) along the vertical axis of the shaft. Scale bar = 500 µm. (from Germain *et al.*, 2016: fig. 1).

In the present study, we provide complementary histological descriptions of the teeth and jaw bones of the shortnose gar, *Lepisosteus platostomus* Rafinesque, 1820, an ichthyophagous fish (Lagler *et al.*, 1942). Our study is essentially based on ground and polished thin sections of bone and dental tissues observed under transmitted natural light as well as microradiographs.

MATERIAL AND METHODS

Material

Lepisosteus platostomus Rafinesque, 1820; 565 mm TL; right and left lower jaws, and dermal scales.

Methods

Ground sections. – The right lower jaw and the anterior part of the left one were dehydrated in graded series of alcohol up to absolute ethanol, then transferred to acetone, and embedded in stratyl polymer (Chronolite 2195). Transverse and longitudinal sections (150-200 µm thick) were made through the right jaw utilizing an Isomet sawing machine and then ground down to 50-75 µm in thickness. The sections were microradiographed with CGR Sigma generator, and then observed under transmitted natural and polarized light under a Zeiss Axiovert 35. Transverse and horizontal sections were also made through the left jaw distal end, and then observed in transmitted natural light.

Some scales were extracted from the right side of the flank, anterior to the dorsal fin. Transverse ground sections of the scales were produced by the same method utilized for the jaws.

RESULTS

Morphology

There are two kinds of teeth in the lower jaws of *Lepisosteus platostomus* according to their height (Figs 1, 2A). They are attached either onto coronoid bones (Fig. 2B) or the dentaries, and are distributed in three rows. The larger teeth are on the labial side of the jaw. They can be separated from each other by a few small teeth (Fig. 2). The largest tooth is on the anterior part of the jaw (Fig. 2A). The smaller teeth form a lingual row, separated from the labial one by a median gutter. Patches of small teeth are found at the top of the lateral side of the jaw (Fig. 2B). The external surface of larger teeth shows thin ridges that nearly reach the base of the apical cap of enamel (Fig. 2A, inset). These large teeth are conical and sharp, and are constituted of a dentine core with an apical cap of enamel, named durodentine (Gross-Lerner, 1957) or acrodin (Ørvig, 1973 *in* Ørvig, 1978a, b) (Fig. 2B-D). The apical region of each tooth is lightly com-

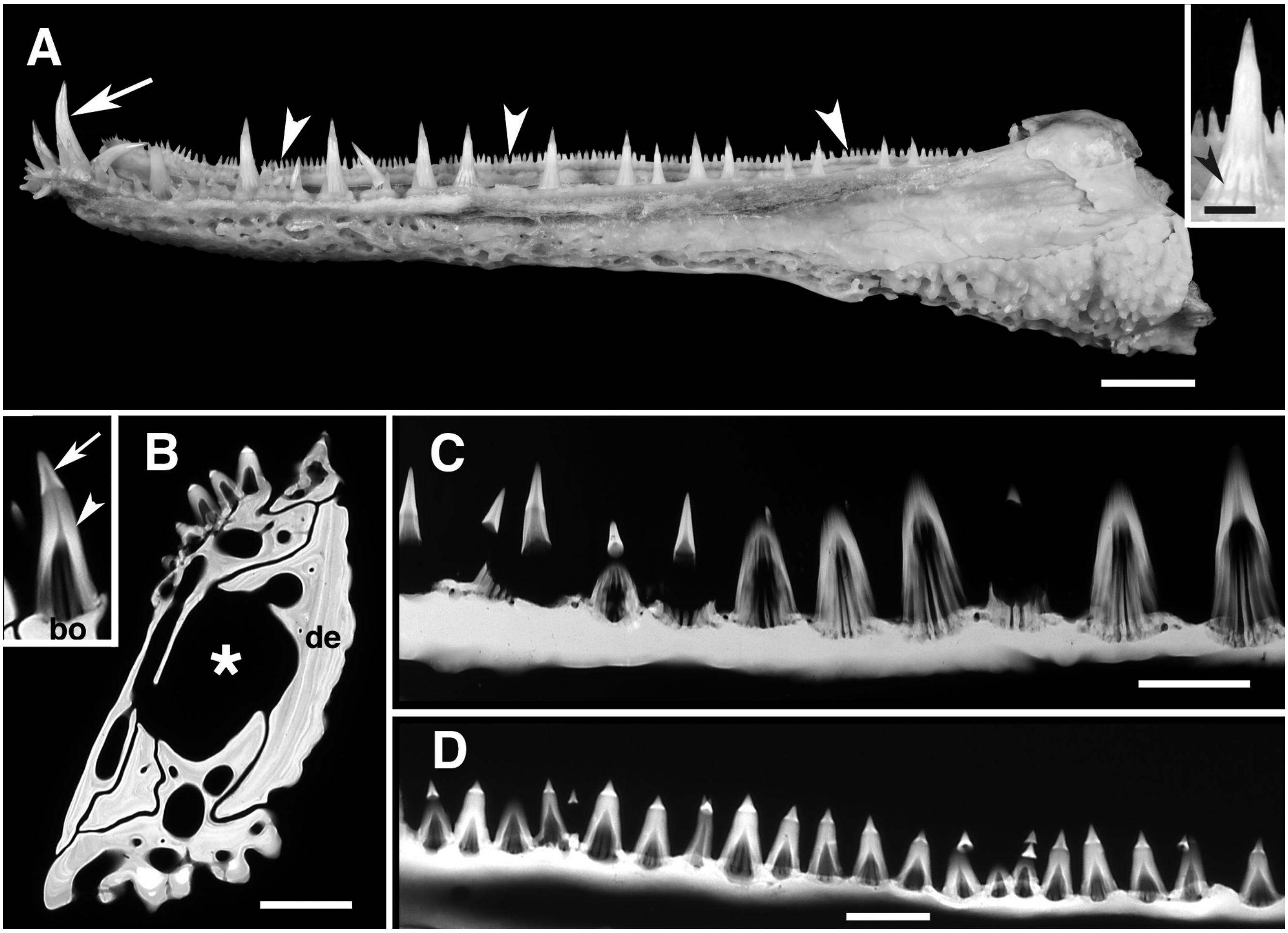

Figure 2. – *Lepisosteus platostomus*. **A**: External view of the left lower jaw showing the caniniform teeth on the labial side of the jaw. The largest tooth (arrow) is located at the anterior tip of the jaw. On the lingual side of the jaw there are small sharp teeth (arrowheads). Scale bar = 5 mm. In the inset a detail of a caniniform tooth showing the external ridges at its base (arrowhead). Scale bar = 1 mm. **B-D**: Right jaw. **B**: Cross section of the jaw (microradiograph) showing five small teeth inserted on a coronoid bone (upper left) plus a larger tooth on the dentary. The white asterisk indicates the unmineralized Meckel's cartilage on the left hand side of the dentary (**de**). Scale bar = 2.5 mm. In the inset a microradiograph of a caniniform tooth and its attachment bone (**bo**), also showing its dentine core (arrowhead) with the apical acrodin cap (arrow). **C**: Parasagittal median section of the jaw (microradiograph) showing five caniniform teeth. The dentine folds occupy the total height of the pulp cavities. On the left one can also see five hypermineralized acrodin caps. Scale bar = 2 mm. **D**: Parasagittal lingual section of the jaw (microradiograph) showing the small lingual teeth series some of them showing minute mineralized folds in the pulp cavity. Scale bar = 1 mm.

pressed with two opposite lateral lancet-like crests. These teeth are typically caniniform and are adapted to the ichthyophagous diet of this species. Microradiographs of longitudinal sections reveal that the axial folds covering the walls of pulp cavities are mineralized (Fig. 2C, D).

Histology

Teeth

Teeth are constituted of a cone of orthodentine covered by an apical cap of enameloid (Fig. 3A). Collar enamel covers the tooth shaft (Fig. 3A, C). Dentine tubules extend nearly to the tooth tip underneath the acrodin cap through a narrow axial canal that extends the pulp cavity (Fig. 3B) beyond the tooth shaft. The wall of the pulp cavity is radially folded. Both the collar enamel and the dentine layers are jointly affected (Fig. 3C). The small teeth have the same organization as the large teeth, but they only possess minute dentine folds on the wall of the pulp cavity (Fig. 3D).

Bone

The osseous tissues in the jaw bones (Fig. 4A, D) show long canaliculi of Williamson[1] that cross the bone lamellae

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[1] The name "canaliculi of Williamson" has been proposed by Tretjakoff (1930) and accepted by the scientific community. It is synonymous to "lepidine tubules" of Williamson (1849), "lepidosteoid tubules" of Goodrich (1913), and "non vascular canals of Williamson" of Ørvig (1951). So we will use this name in our text.

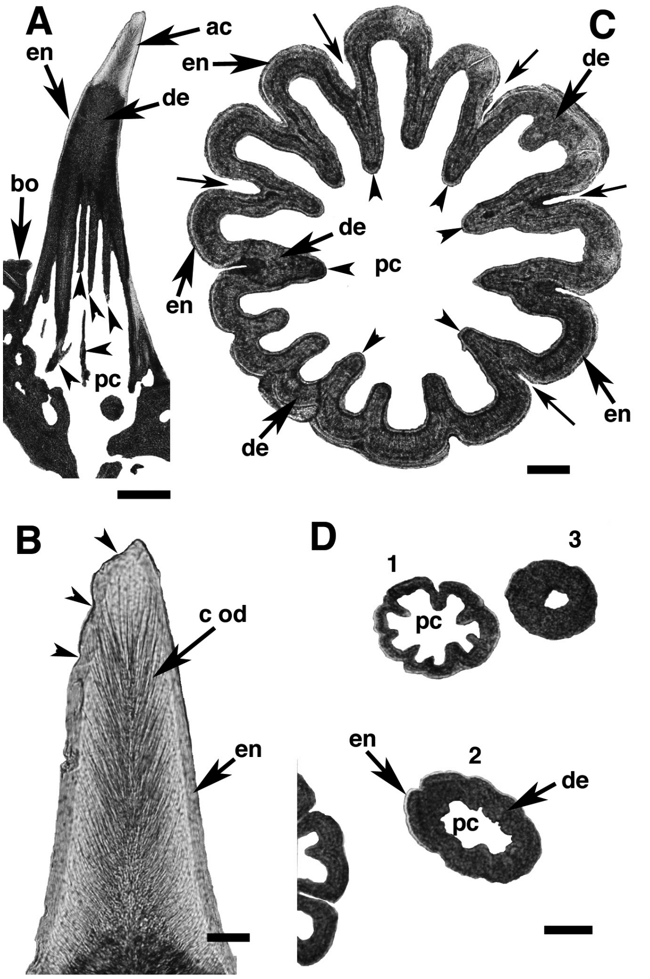

Figure 3. – *Lepisosteus platostomus*. Left jaw. **A**: Axial section of a caniniform tooth showing the apical cap of acrodin (**ac**) above the dentine cone (**de**), the collar enamel (**en**) that covers the tooth shaft, the dentine folds in the pulp cavity (**pc**), and the coronoid bone (**cb**). Scale bar = 500 µm. **B**: Detail of the apex of the tooth showing the odontoblastic canaliculi (arrow). Scale bar = 20 µm. **C**: Transverse section of a caniniform tooth showing the external ridges (arrows) and the dentine folds (arrowheads) in the pulp cavity (**pc**). The dentine is overlain by a thin collar enamel (**en**) covering the tooth shaft and participating in the folds. Scale bar = 100 µm. **D**: The section crosses through three small lingual teeth that show minute folds in their pulp cavity. A caniniform tooth can be seen at the bottom left. Scale bar = 50 µm.

more or less at right angles. These canaliculi open either at the bone surface of the primary bone, or at the surface of the trabeculae in secondary bone (Fig. 4B, C). They are more sinuous in the coronoid bones and they are frequently branched (Fig. 4C). The apical end of the canaliculi of Williamson show very thin branching (not illustrated). The osseous tissues of the various bones in the jaws show star-shaped osteocytes with ramified processes that spread in between lamellae of the bony tissue (Fig. 4E, F). Reversal cementing lines indicate that the bone tissue was remodelled here and there, especially in the vicinity of tooth bases (Fig. 4B, F).

In the dermal scales, canaliculi of Williamson are relatively straight and they are rarely branched (Fig. 4D).

DISCUSSION

Since the proposal of Holostei as a taxonomic unit by Müller (1844), at that time yet including polypterids, the holostean monophyly has been the subject of several studies. Huxley (1861) removed polypterids from this group and the holosteans, as such, were thereafter generally accepted (*cf.* Nelson, 1969a, 1969b; Jessen, 1973). However, in the early 1970s, Patterson (1973) proposed the Holostei as a paraphyletic group. The lepisosteiforms are the sister-group of a clade formed by *Amia* + teleosts, named the Halecostomi. This proposal was accepted until the end of the 20th century (Wiley, 1976; Gardiner *et al.*, 1996; Grande and Bemis, 1998).

The validity of Halecostomi, and the revalidation of Holostei were firstly proposed based on molecular studies (Normark *et al.*, 1991; Inoue *et al.*, 2009) then corroborated by morphological study of the Lepisosteiformes by Grande (2010). Therefore, the holosteans were restored as a monophyletic group.

Among the characters defining the Lepisosteidae, two are significant and constitute a guiding thread of our histological study: 1) the presence of canaliculi of Williamson in bone tissues, and 2) plicidentine found in all teeth in this group.

The bone tissues of Lepisosteidae possess both canaliculi of Williamson and osteocytes (Williamson, 1849; Hertwig, 1879; Nickerson, 1893; Stephan, 1900; Goodrich, 1913; Ørvig, 1951; Sire and Meunier, 1994; Brito *et al.*, 2000) like the numerous taxa that are currently ascribed to the Holostei (Goodrich, 1913; Aldinger, 1937; Ørvig, 1951; Schultze, 1966, 1977; Meunier *et al.*, 1988; Meunier and Gayet, 1992; Gayet and Meunier, 1993; Thomson and McCune, 1984, 1994; and others). Curiously, the histological characteristic of bony tissues in extant and extinct species more precisely the presence of canaliculi of Williamson containing cytoplasmic processes, are never used in these various modern analyses, which is unfortunate (Meunier, 2011).

Regarding the presence of canaliculi of Williamson in bone tissues, we can note that similar structures considered as typically "holostean" features (Goodrich, 1913; Ørvig, 1951; Sire and Meunier, 1994; Schultze 1996; Meunier, 2011) are found in the ganoid scales of ginglymods, halecomorphs, and in teleosteomorphs such as pholidophorids (Schultze, 1966, 1996) and aspidorhynchids (Schultze 1966; Brito and Meunier, 2000). These structures are also found in the bones of extant holosteans (Lepisosteidae and Amiidae). In contrast, canaliculi of Williamson are neither found

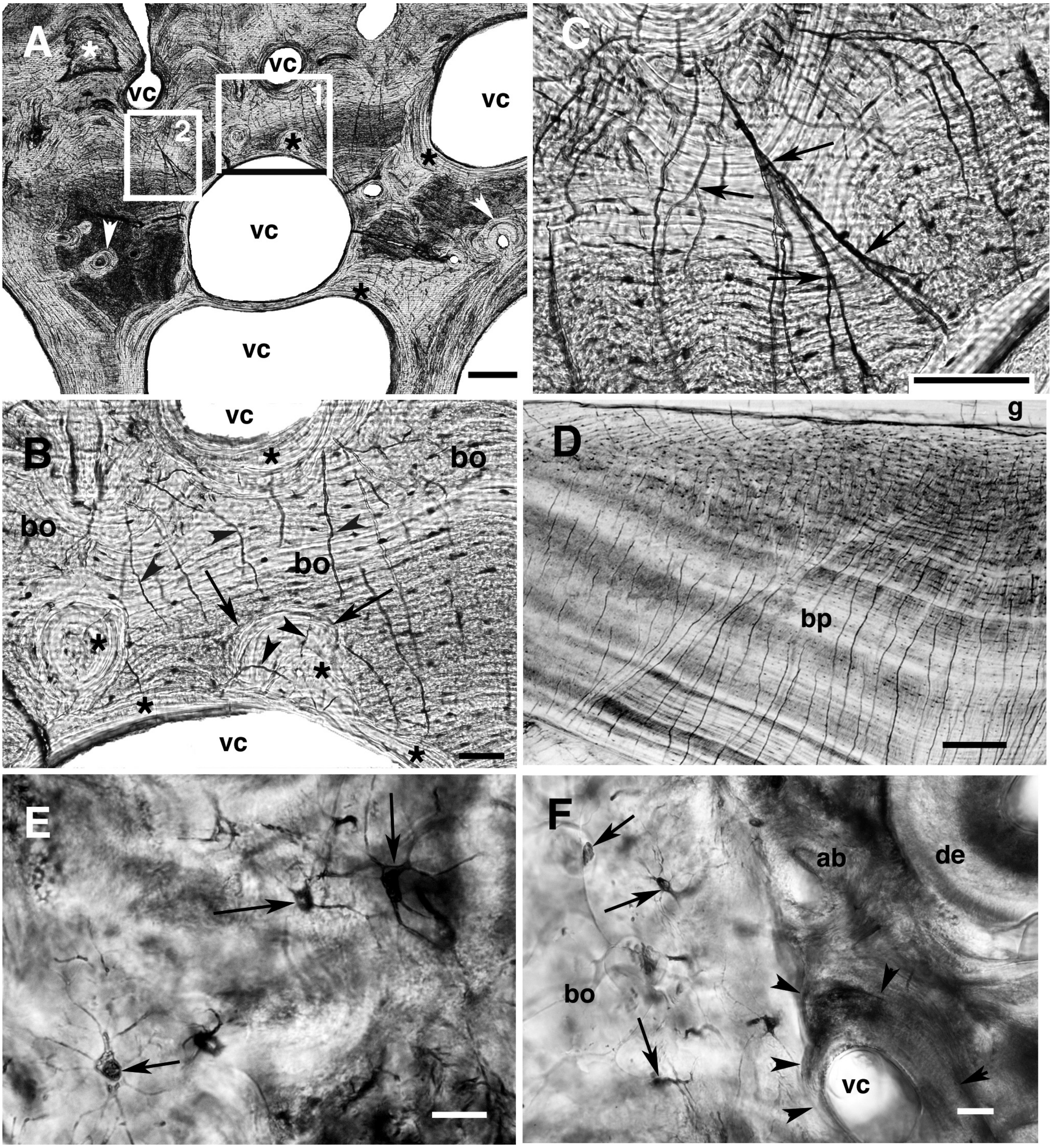

Figure 4. – *Lepisosteus platostomus*. **A-C**: Lower right jaw, transverse sections, natural transmitted light. **A**: Dentary. Primary bone with canaliculi of Williamson is dominating but with some areas of secondary bone around some vascular cavities. A patch of multilayered ganoine is seen (white asterisk) and the white arrowheads point to small secondary vascular canals. Scale bar = 50 µm. **B**: Detail of the inset 1 of Fig. 4A showing primary bone (**bo**) and secondary bone (black asterisks) with canaliculi of Williamson (arrowheads) present in the two types of bone tissues. Scale bar = 50 µm. **C**: Detail of the inset 2 of Fig. 4A showing several ramified canaliculi of Williamson (arrowheads). Scale bar = 50 µm. **D**: Scale. Transverse section, natural transmitted light. The bony basal plate (**bp**) shows the canaliculi of Williamson that are relatively parallel and with very few branchings. (**G** = ganoine). Scale bar = 200 µm. **E**: Coronoid bone. Detail of bony tissue showing several osteocytes (arrows) with their canaliculi. Scale bar = 10 µm. **F**: Coronoid bone. Detail of the base of a tooth (**de**) showing attachment bone (**ab**), primary bone (**bo**) and a vascular canal (**vc**) surrounded by secondary bone that is discordant (arrowheads) relatively to the primary bone. Scale bar = 5 µm.

in palaeoniscoids, nor in fossil and extant polypterids, nor in teleosts and in elasmoid amioid scales.

Regarding the presence of plicidentine in Lepisosteidae, it is significant that extant Lepisosteidae are ichthyophagous predators considered as ram feeding fishes (Porter and Motta, 2004). They have elongate, fusiform bodies similar in morphology to that of pikes (Esocidae) that also show a predatory behaviour (Webb *et al*., 1992); they are both fast-starts and steady swimming fishes (Lauder and Norton, 1980; Webb *et al*., 1992; Long *et al*., 1996). The elongate jaws of gars bear numerous sharp teeth that present similar characteristics to Lepisosteidae, especially an apical cap of acrodin (Peyer, 1968; Schmidt, 1971), and the plicidentine organization on the wall of the pulp cavity (Tomes, 1878: fig. 12; Peyer, 1968: pl. 28b; Schultze, 1969: pl. 1-fig. 6). In lepisosteid teeth, the plicidentine is constituted of radial infolding of the wall of the tooth pulp cavity (Germain *et al*., 2016) (see Fig. 1).

The histological structure of lepisosteid teeth, with their cone of orthodentine covered by an apical hypermineralized cap of acrodin and surrounded by a relatively thin layer of collar enamel was described by Prostak *et al*. (1989), Ishiyama *et al*. (1999) and Sasagawa *et al*. (2012, 2014). Curiously, the teeth look superficially like the odontodes on the surface of the dermal scales (Nickerson, 1893; Schmidt, 1971), except for the internal organization of the pulp cavity that is folded only in the teeth, not anywhere on the scales. At the tooth base, the external surface is finely striated, especially on the fangs. Folded internal walls of the basal region of the pulp cavity of oral teeth in lepisosteids characterize the plicidentine organization of orthodentine (Tomes, 1878), and our study confirms the observations made by previous authors (Peyer, 1968; Schultze, 1969; Grande, 2010; Germain *et al*., 2016). Plicidentine is also found in Crossopterygii and in numerous extinct and extant reptiles (Lison, 1954; Peyer, 1968; Schultze, 1970; Kearney and Rieppel, 2006; Maxwell *et al*., 2011a, b; and many others). Among Actinopterygii, plicidentine seems to be much scarce. It was thought to occur in lepisosteids only (Owen, 1841 *in* Tomes, 1878; Peyer, 1968; Schultze, 1969; Grande, 2010; Germain *et al*., 2016). However, true plicidentine organization of dental orthodentine has recently been described in the teeth of several predatory teleostean fishes. It occurs in the teeth of the lingual dental plate of *Arapaima gigas*, an Osteoglossomorpha (Meunier *et al*., 2013), and in the labial teeth of *Hoplias aimara*, a Characiforme (Erythrinidae) (Meunier *et al*., 2015); it is also presumably present in the teeth of several predatory Characidae (Characiformes) (Meunier *et al*., 2015). The basal part of the teeth of the angler fish (*Lophius piscatorius* Linnaeus, 1758) is partly constituted of plicidentine (Meunier, 2015), as well as those of the wolffish (*Anarhichas denticulatus* Krøyer, 1845) (Meunier and Germain, unpubl. obs.).

Schultze (1969, 1970) had described three types of plicidentine. The teeth of *Lepisosteus platostomus* fall into the polyplocodonte type: pulp cavity filled with primary folding of orthodentine with collar enamel extending between folds. The plicidentine of *L. platostomus* is far more complex than that found in teleostean teeth because in the latter, the external hypermineralized layer of enamel does not enter the folds, at least not in the species studied to date (Meunier, 2015; Meunier *et al*., 2015; Germain *et al*., 2016).

CONCLUSION

We consider that the presence of canaliculi of Williamson in bone tissues is a good indication of systematic affinity to the clade Holostei, including here the ganoid teleosteomorphs. For holostean fishes, the presence of plicidentine in teeth can be an indication of an affinity to the Lepisosteidae family, and suggests a predatory diet for extant and extinct lepisosteids. However, the type of plicidentine appears to be related to the biting mode and is not a phylogenetically stable character.

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REFERENCES

AGASSIZ L., 1833-1844. - Recherches sur les Poissons fossiles. 5 volumes & atlas. Imprimerie Petitpierre, Neuchâtel.

Aldinger H., 1937. - Permische Ganoidfische aus Ostgrönland. *Medd. Grönl*., 102: 1-392.

BRITO P.M. & MEUNIER F.J., 2000. - The morphology and histology of the scales of Aspidorhynchids (Actinopterygii, Halecostomi) and their phylogenetical implications. *Geobios,* 33: 105-111.

BRITO P.M., MEUNIER F.J. & GAYET M., 2000. - The morphology and histology of the scales of the Cretaceous gar *Obaichthys* (Actinopterygii, Lepisosteidae): phylogenetic implications. *C.R. Acad. Sci. Paris*, 331: 823-829.

BRITO P.M., AMARAL C.R.L. & MACHADO L.P., 2006. - A ictiofauna do Grupo Bauru, Cretáceo Superior da Bacia Bauru, Sudeste do Brasil. *In*: Paleontologia de Vertebrados: Grandes Temas e Contribuições científicas (Galo V., Brito P.M., Silva H.M. & Figueiredo F.S., eds), pp. 133-143. Rio de Janeiro: Editora Interciência.

BRITO P.M., LINDOSO R., CARVALHO I.S. & MACHADO G.P., 2016. - Discovery of †Obaichthyid gars (Holostei, Ginglymodi, Lepisosteiformes) in the Aptian Codo Formation of the Parnaiba Basin: remarks on paleobiogeographical and temporal range. *Cretaceous Res*., 57(3): 10-17.

CAVIN L., 2010. - Diversity of Mesozoic semionotiform fishes and the origin of gars (Lepisosteidae). *Naturwissenschaften*, 97: 1035-1040.

CAVIN L., DEESRI U. & SUTEETHORN V., 2013. - Osteology and ships of *Thalichthys* nov. gen.: a Gynglymodi from the Late Jurassic-Early Cretaceous of Thailand. *Palaeontology*, 56(1): 183-208.

FRIEDMAN M., 2015. - The early evolution of ray-finned fishes. *Palaeontology*, 58: 213-228.

FROESE R. & PAULY D., 2016. FishBase. World Wide Web electronic publication.www.fishbase.org. Accessed Jan. 2016.

GARDINER B., MAISEY J.G. & LITTLEWOOD D.T.J., 1996. - Interrelationships of basal neopterygians. *In*: Interrelationships of Fishes (Stiassny M.L.J., Parenti L.R. & Johnson G.D., eds), pp. 117-146. Academic Press, San Diego.

GAYET M. & MEUNIER F.J., 1993. - Conséquences paléobiogéographiques et biostratigraphiques de l'identification d'écailles ganoïdes du Crétacé supérieur et du Tertiaire inférieur d'Amérique du Sud. *Doc. Lab. Géol. Lyon*, 125: 169-185.

GERMAIN D., MONDÉJAR-FERNÁNDEZ J. & MEUNIER F.J. 2016. - The detection of plicidentine tooth organisation in teleostean fishes through non-destructive tomography. *Cybium,* 40(1): 7-22.

GOODRICH S., 1913. - On the structure of bone in fishes: a contribution to paleohistology. *Proc. Zool. Soc. Lond.*, 1913: 80-85.

GRANDE L., 2010. - An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. American Society of Ichtyology and Herpetology, Spec. Publ 6. *Copeia,* 10(2A): 871.

GRANDE L. & BEMIS W.E., 1998. - A comprehensive phylogenetic study of Amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. Soc. Verterbr. Paleontol., Mem. 4. *J. Vertebr. Paleontol.,* 18(1): 690 p.

GROSS-LERNER H., 1957. - Über Bau und Entwicklung der Reusenzähne von *Cetorhinus maximus* Gunner. *Z. Zellforsch.*, 46(3): 357-368.

HERTWIG O., 1879. - Ueber das Hautskelet der Fische. 2 : Das Hautskelet der Ganoiden (*Lepidosteus* und *Polypterus*). *Morphol. Jahrb.*, 5: 1-21.

HURLEY I.A., LOCKRIDGE MUELLER R., DUNN K.A., SCHMIDT E.J. & FREIEDMAN M., 2007. - A new time-scale for ray-finned fish evolution. *Proc. R. Soc., B.*, 274: 489-498.

HUXLEY E., 1861. - Preliminary essay upon the systematic arrangement of the fishes of the Devonian epoch. *Mem. Geol. Survey UK*, 10: 1-40.

INOUE J.G., KUMAZAWA Y., MIYA M. & NISHIDA M., 2009. - The historical biogeography of the freshwater knifefisches using mitogenomic approaches: a Mesozoic origin of the Asian notopterids (Actinopterygii: Osteoglossomorpha). *Mol. Phylogenet. Evol.*, 51: 486-499.

ISHIYAMA M., INAGE T. & SHIMOKAWA H., 1999. - An immunocytochemical study of amelogenin proteins in the developing tooth of the gar-pike, *Lepisosteus oculatus* (Holostei, Actinopterygii). *Arch. Histol. Cytol.*, 62: 191-197.

JESSEN H., 1973. - Interrelationships of actinopterygians and brachiopterygians: evidence from pectoral anatomy. *In*: Interrelationships of Fishes (Greenwood H., Miles R.S. & Patterson C., eds). *J. Linn. Soc.*, 53(suppl. 1): 227-232.

KEARNEY M. & RIEPPEL O., 2006. - An investigation into the occurrence of plicidentine in the teeth of Squamate Reptiles. *Copeia,* 3: 337-350.

LAGLER K.F., OBRECHT C.B. & HARRY G.V., 1942. - The food and habits of gars (*Lepisosteus* spp.) considered in relation to fish management. *Invest. Indiana Lakes Streams*, 2: 117-135.

LAUDER G.V. & NORTON S.E., 1980. - Assymetrical muscle activity during feeding in the gar, *Lepisosteus aculeatus*. *J. Exp. Biol.*, 84: 17-32.

LISON L., 1954. - Les dents. *In*: Traité de Zoologie (Grassé P.P., ed.), Vol. 12, pp. 791-853. Masson, Paris.

LONG J.H. Jr., HALE M.E., MCHENRY M.J. & WESTNEAT M.W., 1996. - Function of fish skin: flexural stiffness and steady swimming of longnose gar *Lepisosteus osseus*. *J. Exp. Biol.*, 199: 2139-2151.

LÓPEZ-ARBARELLO A., 2012. - Phylogenetic interrelationships of Ginglymodian fishes (Actinopterygii: Neopterygii). *PloS ONE*, 7(7): e39370.

MAXWELL E.E., CALDWELL M. & LAMOUREUX D.O., 2011a. - The structure and phylogenetic distribution of amniote plicidentine. *J. Vertebr. Paleontol.*, 31(3): 553-561.

MAXWELL E.E., CALDWELL M. & LAMOUREUX D.O., 2011b. - Tooth histology attachment, and replacement on the Ichthyopterygia reviewed in an evolutionary context. *Paläontol. Z.*, 86(1): 1-14 p.

MEUNIER F.J., 2011. - The Osteichtyes, from the Paleozoic to the extant time, through histology and paleohistology of bony tissues. *C. R. Palevol.*, 10: 347-355.

MEUNIER F.J., 2015. - New data on the attachment of teeth in the Angler fish *Lophius piscatorius* (Actinopterygii; Teleostei; Lophiidae). *Cah Biol. Mar.*, 56(2): 97-104.

MEUNIER F.J. & GAYET M., 1992. - Remaniement de la ganoïne chez un Semionotidae du Crétacé supérieur de Bolivie : intérêt paléobiologique. *Geobios*, 25: 767-774.

MEUNIER F.J., GAYET M., GÉRAUDIE J., SIRE J.Y. & ZYLBERBERG L., 1988. - Données ultrastructurales sur la ganoïne du dermosquelette des actinoptérygiens primitifs. *Mém. Mus. Natl. Hist. Nat., Paris*, 53: 77-83.

MEUNIER F.J., BRITO P.M. & LEAL M.E., 2013. - Morphological and histological data on the structure of the lingual tooth plate of *Arapaima gigas* (Osteoglossidae; Teleostei). *Cybium,* 37(4): 263-271.

MEUNIER F.J., DE MAYRINCK D. & BRITO P.M., 2015. - Presence of plicidentine in the labial teeth of *Hoplias aimara* (Erythrinidae; Ostariophysi; Teleostei). *Acta Zool.*, 96(2): 174-180.

MÖLLER W., 1940. - Zur Krenntnis des Kiefergebisses und der Zähne von *Lepisosteus* und *Amia*. *Z. Mikr. Anat. Forsh.*, 48: 607-630.

MÜLLER J., 1844. – Ueber den Bau und die Grenzen der Ganoiden und über des natürliche System der Fische. *Phys. Math. Abn. Akad. Wiss. Berlin*, 1844: 117-216; 416-422.

NELSON G.J., 1969a. - Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bull. Am. Mus. Nat. Hist.*, 141(4): 477-552.

NELSON G.J., 1969b. - Origin and diversification of teleostean fishes. *Am. N.Y. Acad. Sci.*, 167(1): 18-30.

NELSON J.S., GRANDE T.C. & WILSON M.V.H., 2016. - Fishes of the World. 5th edit., 752 p. Wiley.

NICKERSON W.S., 1893. - The development of the scales of *Lepidosteus*. *Bull. Mus. Comp. Zool. Harvard Coll.*, 24(5): 115-139.

NORMARK B.B., MCCUNE A.R. & HARRISSON R.G., 1991. - Phylogenetic relationships of neopterygian fishes, inferred from mitochondrial sequences. *Mol. Biol. Evol.*, 8(6): 819-834.

ØRVIG T., 1951. - Histologic studies of placoderms and fossil elasmobranches. The endoskeleton with remarks on the hard tissues of lower vertebrates in general. *Ark. Zool.*, (ser 2)2: 321-354.

ØRVIG T., 1978a. - Microstructure and growth of the dermal skeleton in fossil actinopterygian fishes: *Bigeria* and *Scanilepis*. *Zool. Scripta*, 7: 33-56.

ØRVIG T., 1978b. - Microstructure and growth of the dermal skeleton in fossil actinopterygian fishes: *Nephrotus* and *Colobodus*, with remarks on the dentition in other forms. *Zool. Scripta*, 7: 297-326.

PATTERSON C., 1973. - Interrelationships of Holosteans. *In*: Interrelationships of Fishes. (Greenwood P.H., Miles R.S. & Patterson C., eds). *Zool. J. Linn. Soc.*, 53(suppl. 1): 235-306.

PEYER B., 1968. - Osteichthyes. *In*: Comparative Odontology (Zangerl R., ed.), pp. 80-110. Univ. Chicago Press.

PORTER H.T. & MOTTA P.J., 2004. - A comparison of strike and prey capture kinematics of three species of piscivorous fishes: Florida gar (*Lepisosteus platyrhincus*), redfin needlefish (*Strongylura notata*), and great barracuda (*Sphyraena barracuda*). *Mar. Biol.*, 145: 989-1000.

PROSTAK K., SEIFERT P. & SKOBE Z., 1989. - Ultrastructure of developing teeth in the gar pike (*Lepisosteus*). *In*: Tooth Enamel (Fearnhead R.W., ed.), pp. 188-192. Florence, Yokohama.

SASAGAWA I. & ISHIYAMA M., 2005. - Fine structural and cytochemical mapping of enamel organ during the enameloid formation stages in gars, *Lepisosteus occulatus*, Actinopterygii. *Arch. Oral Biol.*, 50: 373-391.

SASAGAWA I., ISHIYAMA M., YOKOSUKA H., MIKAMI M. & UCHIDA T., 2009. - Tooth enamel and enameloid in actinopterygian fish. *Front. Mater. Sci. China*, 3(2): 174-182.

SASAGAWA I., YOKOSUKA H., ISHIYAMA M., MIKAMI M., SHIMOKAWA H. & UCHIDA T., 2012. - Fine structural and immunohistochemical detection of collar enamel in the teeth of *Polypterus senegalus*, an actinopterygian fish. *Cell Tissue Res.*, 347: 369-381.

SASAGAWA I., ISHIYAMA M., YOKOSUKA H., MIKAMI M., SHIMOKAWA H. & UCHIDA T., 2014. - Immunohistochemical and Western blot analyses of collar enamel in the jaw teeth of gars, *Lepisosteus oculatus*, an actinopterygian fish. *Connect. Tissue Res.*, 55(3): 225-233.

SCHMIDT W.J., 1971. - The normal tooth tissues. *In*: Polarizing Microscopy of Normal and Diseased Dental Tissues in Man and Other Vertebrates (Schmidt W.J. & Keil A., eds), pp. 51-469. Pergamon Press, Oxford-New York.

SCHULTZE H.P., 1966. - Morphologische und histologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Übergang von ganoid- zu Rundschuppen). *N. Jb. Geol. Paläont. Abh.*, 126(3): 232-314.

SCHULTZE H.P., 1969. - Die Faltenzähne der Rhipidisiiden Crossopterygier, der Tetrapoden und der Actinopterygier-Gattung *Lepisosteus* nebst einer Beschreibung der Zahnstruktur von *Onichodus* (Struniiformer Crossopterygier). *Palaeontol. Ital.*, New Ser. 35, 65: 63-137.

SCHULTZE H.P., 1970. - Folded teeth and the monophyletic origin of Tetrapods. *Am. Mus Novitates*, 2408:1-10.

SCHULTZE H.P., 1977. - Ausgansform und Entwicklung der rhombischen Schuppen der Osteichthyes (Pisces). *Paläontol. Z.*, 51: 152-168.

SCHULTZE H.P., 1996. - The scales of Mesozoic actinopterygians. *In*: Mesozoic Fishes: Systematics and Paleoecology (Arratia G. & Viöhl G., eds), pp. 83-93. Dr. F. Pfiel Verlag, München.

SIRE J.Y. & MEUNIER F.J., 1994. - The canaliculi of Williamson in Holostean bone (Osteichthyes, Actinopterygii): a structural and ultrastructural study. *Acta Zool.*, 75: 235-247.

STEPHAN P., 1900. - Recherches histologiques sur la structure du tissu osseux des poissons. *Bull. Sci. Fr. Belg.*, 33: 281-429.

THOMSON K.S. & McCUNE A.R., 1984. - Scale structure as evidence of growth patterns in fossil semionotid fishes. *J. Vertebr. Paleontol.*, 4(3): 422-429.

THOMSON K.S. & McCUNE A.R., 1994. - Development of the scales in *Lepisosteus* as a model for scale formation in fossil fishes. *Zool. J. Linn. Soc.*, 82: 73-86.

TOMES C.S., 1878. - On the structure and development of vascular dentine. *Phil. Trans. R. Soc., Lond.*, 169: 25-47.

TRETJAKOFF D.K., 1930. - Die Hautschuppen der Anamnia. *Zeitschr. Wiss. Zool.*, 136: 319-354.

WEBB P.W., HARDY D.H. & MEHL V.L., 1992. - The effect of armoured skin on the swimming of longnose gar, *Lepisosteus osseus*. *Can. J. Zool.*, 70(6): 1173-1179.

WILEY E.O., 1976. - The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae). *Univ. Kansas Publ., Mus. Nat. Hist., Miscell. Publ.*, 64: 1-111.

WILEY E.O. & SCHULTZE H.P., 1984. - Family Lepisosteidae (gars) as living fossils. *In:* Living Fossils (Eldredge N. & Stanley S.M., eds), pp. 160-165. Springer-Verlag, New-York.

WILLIAMSON W.C., 1849. - On the microscopic structure of the scales and dermal teeth of some ganoid and placoid fish. *Philos. Trans. R. Soc. Lond.*, B, 139: 435-475.